

# Invasion success on European coastal dunes

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## Abstract

Many invasive plants are threatening the already highly vulnerable habitats of coastal dunes in Europe. Setting priority target species to control is mandatory for an effective planning of invasion management strategies at European level. This can be possible after identifying the species that currently have greater invasion success, in consideration of their ecological traits and origin. We quantified the three main components of invasion success for the extra-European alien plants found on European coastal dunes: local abundance, regional distribution and niche breadth, and related them to their life forms and origins. We found that life form was a better predictor of invasion success. In particular, geophytes and therophytes were the species with the greatest invasion success. Quite surprisingly, alien plants from Africa appeared as the group with slightly higher mean invasion success although this result was not statistically significant. We also highlighted the species deserving special attention. Among these, *Xanthium orientale*, *Erigeron canadensis* and *Oenothera* gr. *biennis* showed the widest levels of niche breadth and regional distribution, and had overall the greatest invasion success, but other species also had high levels in one of the three components of invasion success.

## Keywords

alien plants, coastal vegetation, ecological success, generalist species, local abundance, niche breadth, regional distribution, sand dunes

## Introduction

The repeated introduction of alien species is a major component of ongoing global changes and a major threat to global biodiversity (Walther et al. 2009). After their direct or indirect introduction by humans (Rodríguez-Labajos et al. 2009; Pyšek et al. 2010; Tordoni et al. 2020), many plant species become naturalised, overcoming local abiotic and reproductive barriers to establish self-sustained populations. A subset of these spread across considerable distances and become invasive (Richardson et al. 2000), with impacts on wildlife, plant biodiversity, and ecosystem functioning (Vilà et al. 2011; Del Vecchio et al. 2015; Blackburn et al. 2019). Coastal dunes are among the most affected habitats (Heywood 1995; Chytrý et al. 2009), especially in Europe, due to the rapid increase in human settlements and activities (Campos et al. 2004; Carboni et al. 2010; Viciani et al. 2020; Lazzaro et al. 2020). As a con-

sequence, their highly specialised flora is currently under serious threat (Prisco et al. 2020).

As effective invasion management strategies cannot possibly consider the large number of invasive plants currently present on European coastal dunes, a more realistic approach would be to focus management efforts on those aliens which have greater invasion success. The ecological success of introduced species depends on their biological traits, on the pressure of introduced propagules and on local ecosystem invasibility (Lonsdale 1999; Lloret et al. 2005; Catford et al. 2009). It can be quantified with different approaches. For example, Cadotte et al. (2006) used a general value of plant abundance, Selosse et al. (2004) used the measure of biomass, while Dyderski and Jagodziński (2018) considered also plant density. Rabinowitz (1981) introduced a framework (not specific for alien plants) which separates three components of success: local abundance, regional distribution and niche breadth



(narrow niche breadth is proper of a specialist species, wide niche breadth of generalists). However, these components are not always correlated and could be highly variable, making it sometimes difficult to unequivocally identify the most successful aliens. In this sense, other authors proposed to consider these three components together in order to quantify the invasion success (Carboni et al. 2016; Cao Pinna et al. 2020).

Different studies have highlighted the importance of life forms and geographical species origin as factors related to invasion success (van Kleunen et al. 2015; Giulio et al. 2020; Cao Pinna et al. 2020). Life forms (Raunkiaer 1934) are among the most simple but informative ecological traits (Acosta et al. 2006), defining species ecological strategies in an extremely synthetic way. Some plant ecological strategies, associated with specific life forms, can convey an advantage for the ability of introduced species to establish in a coastal ecosystem. If invasion success is related to particular adaptations to the host habitats, we could expect that the most successful alien species would share the life forms that are most common among the native species of European coastal dunes, which tend to be annual species and biennial or perennial herbs (Acosta et al. 2006, Kuiters et al. 2009). However, other authors hypothesized that forms not widely represented among native species, such as woody plants in dune grasslands (Torca et al. 2019), could have the advantage to occupy empty niches (Elton 1958; MacDougall et al. 2009). Indeed, for plant invaders, being different is often equated with being successful (MacArthur and Wilson 1967; Daehler 2001; D'Antonio and Hobbie 2005).

Similarly, considering the geographic origin of successful invasive plants may allow to tune prevention strategies to avoid further introductions. Geographic origin of invasive species depends on different factors (Hayes and Barry 2008). According to the intermediate distance hypothesis (Seebens et al. 2017), we could expect higher invasion success by plant species from regions that are at intermediate distances from the invaded region. Indeed, over short distances, the proportion of potential alien species is low, because the native ranges of many species extend into the target region, where they are thus native. At large distances, the proportion of potential alien species increases, but the probability to be transported by humans and survive transportation decreases. Based on the climatic similarity hypothesis instead, the species coming from regions with similar climatic conditions are preadapted to successful invasions, for example those exchanged between North America and Europe, both located in temperate climates. At the same time, climatic similarity between regions favours the exchange of people and goods (Tatem and Hay 2007), which also favours biological introductions (Wilson et al. 2009; Seebens et al. 2015). An alternative hypothesis is that the regions richer in biodiversity, such as those at the tropics and in the southern hemisphere, have more chance to donate more species (van Kleunen et al. 2015), and hence more probability that a higher number of species have greater invasion success.

In a previous study, Giulio et al. (2020) provided a comprehensive assessment of alien plant invasions in the coastal dunes across Europe, highlighting that coastal dunes should be in the focus of European invasion management strategies. However, we still need to understand which factors are more important in the shaping of invasion pathways. On these bases, in this study we analysed the invasion success of alien species on the coastal dune habitats of Europe. To this aim we used data from the European Vegetation Archive (EVA) to quantify the invasion success based on Rabwinowits' approach which is based on three components of alien success: local abundance, regional distribution and niche breadth. Moreover, we were interested in investigating the invasion success in relation to life forms and geographical origins.

## Methods

### Study area

Our study focuses on the two most characteristic and dynamic habitat types in the coastal dune vegetation zonation (Marcenò et al. 2018): B1.3. Shifting coastal dunes and B1.4. Coastal stable dune grasslands (grey dunes), according to the habitat classification of the European Nature Information System (EUNIS; Janssen et al. 2016). Shifting coastal dunes (B1.3) are partly covered by open grasslands, modelled by wind and occasionally subjected to inundation by tides and waves. Stable dune grasslands (B1.4) are covered mainly by perennial grasses, forbs, low shrubs and succulent plants. The study area includes all the European coastal dune systems, depending on data availability (Figure 1). In addition, we also considered the non-European coasts of the Mediterranean Sea and Black Sea.

### Data collection

An initial dataset of 23,446 georeferenced vegetation plots (relevés) containing 2,035 vascular plant species with cover values was extracted from EVA (Chytrý et al. 2016). We selected all plots corresponding to the phytosociological classes (vegetation types) of coastal dune vegetation, i.e., *Ammophiletea*, *Honckenyo-Elymetea arenarii* and *Koelerio-Corynephoretea canescentis pro parte* (embryonic, mobile and semifixed dunes). We identified the alien species mainly through the DAISIE (2009) European Invasive Alien Species Gateway and other sources (Pagad et al. 2018; EASIN 2021). We considered only neophytes (alien plants introduced after 1500; Pyšek and Jarošík 2005) from outside of Europe (excluding those bordering the Mediterranean Basin, i.e. from North Africa and the Middle East), and selected just plots including at least one of them. Also, we selected only plots recorded after 1970, obtaining 2,153 plots (Fig. 1) and 89 alien species (for details, see Giulio et al. 2020). Plot size mostly ranged between 3 and 100 m, however, note that the analysis performed in



this study are not dependent on plot size. Alien species were further grouped into five categories, according to their geographic origin (African, North American, Central and South American, East Asian and Oceanian). We also sorted the alien species according to their life form, including Chamaephytes, Geophytes, Hemicryptophytes, Phanerophytes and Therophytes (Raunkiaer 1934). When a species was known to be associated with more than one region of origin or more than one life form, all possible categories were considered.

## Data analysis

We applied the Rabinowitz's classification of rarity and abundance (Rabinowitz 1981; Carboni et al. 2016) on our list of alien plant species, considering three indices: (1) local abundance, (2) regional distribution and (3) niche breadth.

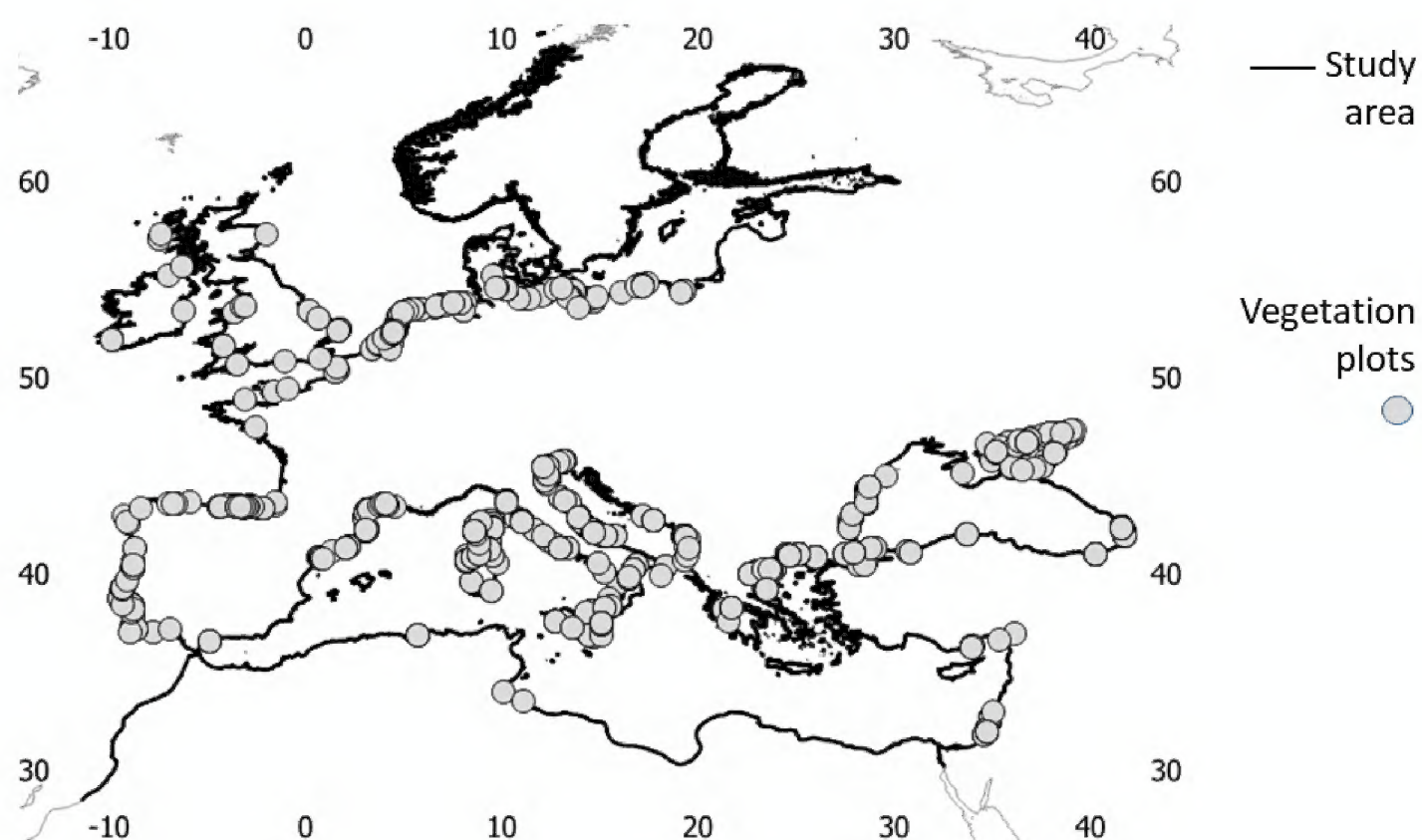
(1) Local abundance was taken from the average percentage cover of each alien species within the plots where it occurred. To calculate it, we first converted the Braun-Blanquet cover classes to cover percentages using the median value of the corresponding class of cover percentage, then we calculated the mean for each species.

(2) to quantify the regional distribution of each alien plant in the study area, we calculated the species' frequency of occurrence. To calculate it, we counted the number of plots where each alien species occurred. Because few species had an extremely high number of occurrences compared to most, we performed a logarithmic transformation. This measure was strongly correlated with geographical spread (calculated as a multiplication between the latitudinal and the longitudinal range to approximate the area of a rectangular polygon encompassing all occurrence points).

(3) To calculate the niche breadth, we extracted, for each alien plant location, the value of two climatic variables, annual temperature and annual precipitation, at a spatial resolution of ~1 km (Karger et al. 2017) and three soil variables, sand fraction, organic carbon content, and pH, at ~250 m resolution (Hengl et al. 2017). These environmental data were those with the smallest resolution available at the European scale applied here. We believe they are a feasible approximation for a continental scale study. Then, we standardized these values and used them to calculate the hypervolume of environmental space occupied by each species (Blonder et al. 2014). In this case also, because few species had an extremely high number of occurrences compared to most, we performed a logarithmic transformation. Large values of hypervolume indicate that the species occupies many different environmental conditions (wide niche breadth), while small values indicate a more specialized species consistently occurring in sites with similar conditions (narrow niche breadth).

We also used these three indices to calculate a synthetic index of success through a PCA (Fig. 2). Because these indices were positively correlated to the first Principal Component, explaining 55% of variance, we used the scores of the first axis as index of success, considering the highest values as highest and the lowest ones as lowest success. Niche breadth and regional distribution had stronger correlation with the first principal component, hence they contributed most in the definition of overall invasion success than local abundance.

Finally, we performed a Kruskal-Wallis test for non-parametric distributions to check if there was an effect of alien species' life forms and origins on the invasion success' components, followed by a pairwise comparison test with Bonferroni correction between life forms and origins to identify significantly different pairs. All analyses were performed in the R software (R Core Team 2020).



**Figure 1.** Study area and location of the vegetation plots used in the analysis.

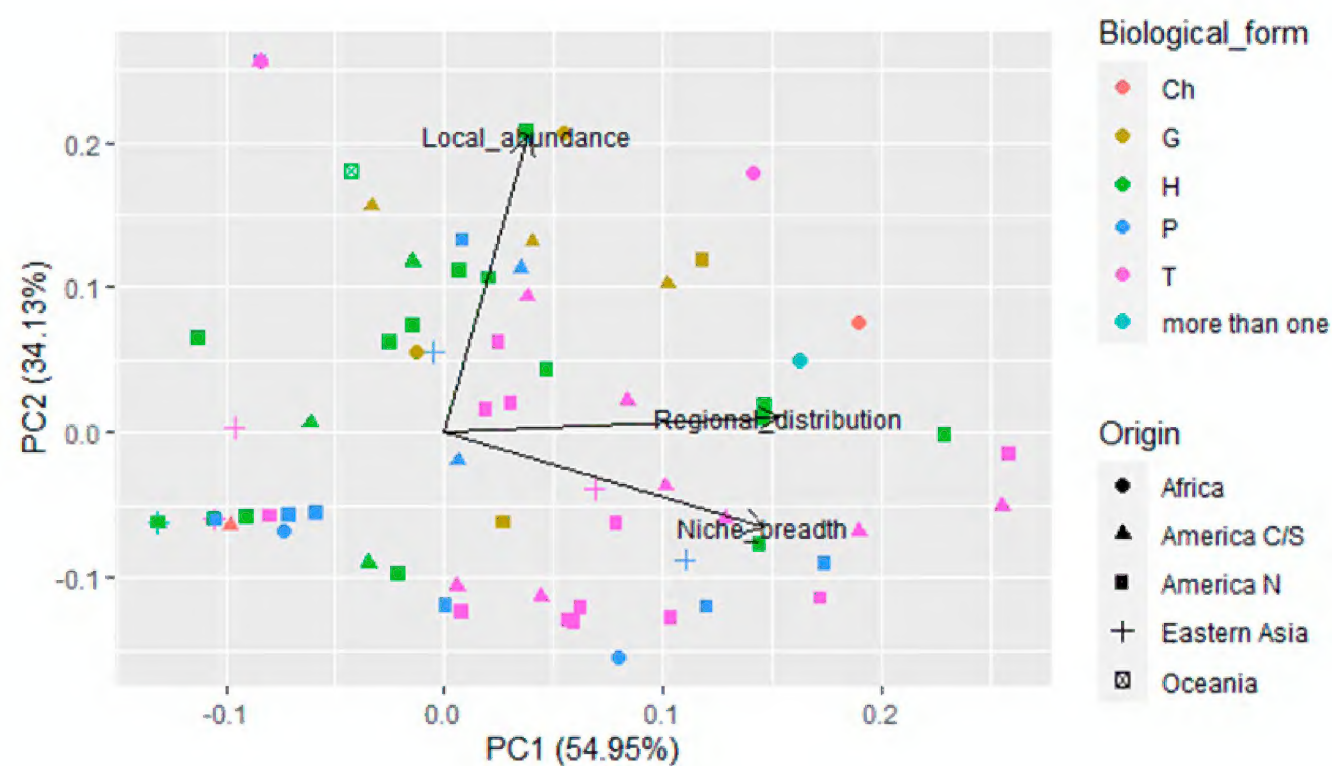


## Results

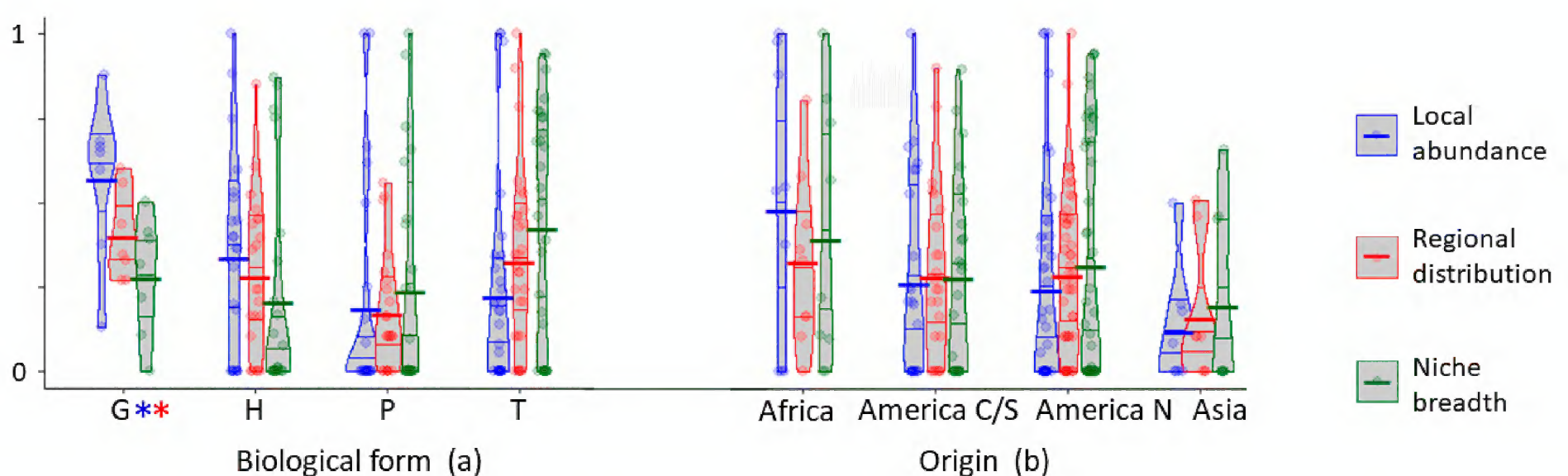
The Kruskal-Wallis test highlighted that life forms had a statistically significant effect on local abundance, on regional distribution, and on the general invasion success, but not on niche breadth (Table 1). Geophytes had higher local abundance compared to phanerophytes (Fig. 3A) and therophytes, and also higher regional distribution with respect to phanerophytes. According to the synthet-

ic index of ecological success, geophytes and therophytes showed the highest mean invasion success, but comparisons with the other groups were not statistically significant (Fig. 4A). Species from Africa showed the highest mean invasion success, although species origins did not have any statistically significant effects (Fig. 4B).

The species which showed the greatest invasion success was *Xanthium orientale*, followed by *Erigeron canadensis* and *Oenothera gr. biennis* (Appendix II). All these three



**Figure 2.** Principal component analysis performed to calculate the synthetic index of invasion success. The scatterplot of alien species is distributed in relation to the three vectors representing the three components of invasion success projected along the first and second components. Ch = chamaephyte; G = geophyte; H = Hemicryptophyte; P = phanerophyte; T = therophyte; more than one = species able to exist under more than one life form. Africa = species from Africa (excluding Northern Africa); America C/S = species from Central or South America; America N = species from North America; Eastern Asia = species from Eastern Asia (for example from India, China or Japan); Oceania = species from Australia and surrounding regions. Correlation matrix between variables and axis are showed in appendix S1 of Supporting information.



**Figure 3.** Violin plots of the three components of ecological success related to (a) life forms and (b) species' origins. Values were rescaled between 0 and 1 (by subtracting the minimum and dividing by the range) for comparability. Bold segment shows the mean and fine segments the quantiles. Asterisks highlight the groups with significantly higher values than other groups according to pairwise Wilcoxon test with Bonferroni correction (Local abundance of G > P, p-value = 0.026; G > T, p-value = 0.041; Regional distribution of G > P, p-value = 0.024). Oceanian origin and chamaephyte group were not represented in these graphs because they included a small number of species (respectively only one and three species). G = geophytes, H = hemicryptophytes, P = phanerophytes, T = therophytes.



species had very wide niche breadth and regional distribution, but low local abundance. The species with the widest niche breadth was *Gomphocarpus fruticosus*. Other species with wide niche breath were *Amorpha fruticosa*, *Ambrosia artemisiifolia* and *Helianthus annuus*, while other species with wide regional distribution were *Carpobrotus* spp. and *Xanthium strumarium*. *Carpobrotus* also had intermediate levels of local abundance and niche breadth, and *Xanthium strumarium* wide niche breadth. The other species with high invasion success had wide niche breadth, intermediate levels of regional distribution, and in some cases also intermediate levels of local abundance, such as *Senecio inaequidens*, *Oenothera drummondii* and *Oenothera glazioviana*. The species with greatest local abundance were *Lepidium densiflorum*, *Amsinckia menziesii*, *Populus trichocarpa*, *Pseudognaphalium undulatum* and *Solanum tuberosum*, but these occurred in no more than one plot across the study area. *Arctotheca calendula* had both very high local abundance and wide niche breadth, while *Paspalum vaginatum* high local abundance and an intermediate level of regional distribution. Also *Lupinus arboreus* and *Epilobium brunnescens* had high local abundance, but low levels of the other components.

*Ambrosia psilostachya* had instead intermediate levels in all the three components.

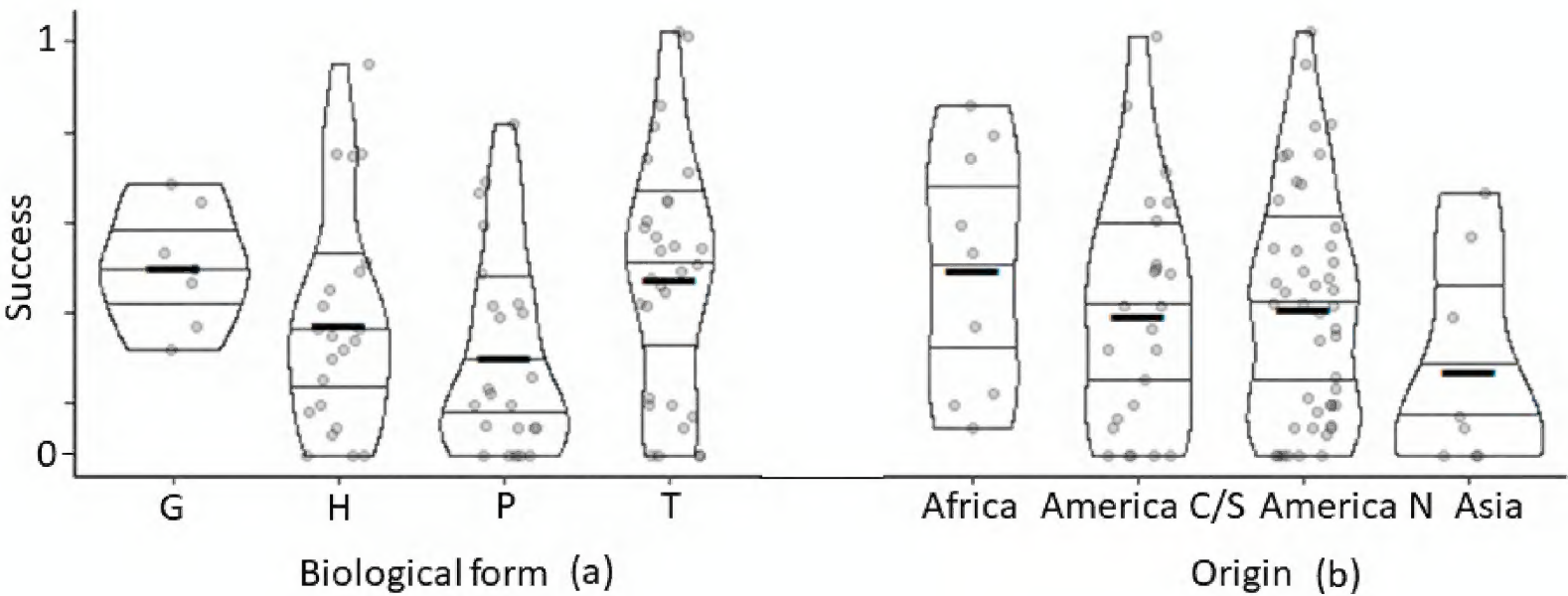
## Discussion and conclusions

In this study we quantified for the first time the main components of invasion success for alien plants from outside of Europe found on European coastal dunes. We observed that geophytes and therophytes were the species with the greatest invasion success, and African alien species were the group with slightly higher mean success. However, many of the alien plants with the highest invasion success were also of North American origin.

Life form confirmed to be a highly informative ecological trait in the coastal environment (Acosta et al. 2006), predicting two components of invasion success, local abundance and regional distribution, and the general index of invasion success. Annual therophytes confirmed to be among the species with most invasion success, reflecting a global invasion pattern (RBG Kew 2016). Their short life cycles and large amount of propagules give annual species more chance to adapt to the highly dynamic and disturbed

**Table 1.** Kruskal-Wallis chi-squared tests of the effect of life form and origin on each component of invasion success.

	Kruskal-Wallis chi-squared test	Degrees of freedom	p-value
<b>Life form</b>			
Local abundance	12.35	3	<b>0.006</b>
Regional distribution	9.06	3	<b>0.029</b>
Niche breadth	4.93	3	0.177
Invasion success	8.10	3	<b>0.044</b>
<b>Origin</b>			
Local abundance	3.79	3	0.285
Regional distribution	2.56	3	0.465
Niche breadth	2.45	3	0.484
Invasion success	3.90	3	0.273



**Figure 4.** Synthetic index of invasion success, related to (a) life forms and (b) species' origins. Values are the normalized first component's scores. Bold segment shows the mean and the other segments the quantiles. Oceanian origin and Chamaephyte group were not represented in these graphs because they included a small number of species (respectively only one and three species). G = geophytes, H = hemicryptophytes, P = phanerophytes, T = therophytes.



coastal dune environment, compared to other life forms (Del Vecchio et al. 2015). Geophytes, although less represented among native coastal dune species than hemicryptophytes and therophytes (Acosta et al. 2006; Torca et al. 2019), also showed high values of invasion success, especially due to high local abundance levels. In fact, geophytes are already known as important weeds worldwide (Sala et al. 2007), first of all because widely introduced as garden ornamentals (Raymond 1996), and also because they are able to accumulate extensive underground reserves which enable them to crowd out native species.

Alien plants from Africa did include more species with high local abundance and consequently this was the group with slightly higher mean invasion success. However, we should note that the relationship between geographic origins and the invasion success of alien plants was not statistically significant. This result confirmed those of Cao Pinna et al. (2020), focused on the Mediterranean part of Europe and remarks that invasion success is not predictable by the species origin at continental scale. A possible explanation could be that species origin is more related to propagule pressure, depending especially on distance and human trade (van Kleunen et al. 2015; Seebens et al. 2015, 2017; Moser et al. 2018), than our three components of invasion success.

The plants with the highest invasion success level (*Xanthium orientale*, *Erigeron canadensis* and *Oenothera gr. biennis*) are all ruderal therophytes or hemicryptophytes from North America. Their invasion has been related to human disturbance (Stanisci et al. 2014). Among the species with wide niche breadth, *Amorpha fruticosa* can be considered as a major threat for the local native coastal biodiversity, altering the soil nitrogen cycle and microbi-

al composition, and consequently related to plant species loss and to shifts in the local species composition (Boscutti et al. 2020). We also found dangerous alien invaders among species with wide regional distributions, such as *Carpobrotus* spp., another “transformer” (Richardson et al. 2000), which specifically alter the levels of pH in the soil and suffocates the local plants of lower cover (Campoy et al. 2018). *Senecio inaequidens* and *Ambrosia artemisiifolia*, showing wide niche breadth and intermediate regional distribution, are instead characterized by high genetic diversity in the invaded ranges (Genton et al. 2005; Monty and Mahy 2009, 2010; Lachmuth et al. 2010). Among them, *Senecio inaequidens* is known to induce changes in the floristic composition of dune vegetation (Heger and Böhmer 2006). Among the species with high local abundance, we mentioned *Arctotheca calendula* (therophyte from Africa), and *Paspalum vaginatum* (geophyte probably originating from Africa; Chen et al. 2005). *A. calendula* is exclusive to dunes, has a successful dispersal mechanism, and is able to rapidly invade on anthropogenically disturbed coasts, especially in the Iberian Peninsula (Campos et al. 2004). *Paspalum vaginatum* is also already known as one of the most dangerous alien species on European coasts, associated to more brackish environments (Filigheddu et al. 2001), often forming dense and tall grasslands, sometimes monospecific or associated with other alien plants (Campos et al. 2004; CABI 2005–2020). *Ambrosia psilostachya*, geophyte from North America, showing intermediate levels of all the three components, colonizes habitats with high levels of human impact (Montagnani et al. 2017), including degraded dunes. Its clonal populations can cover large areas rapidly in France, where it seems to be increasing (Fried et al. 2015).

**Table 2.** Species with most invasion success. Values are scaled between 0 and 1. Ch = chamephyte, G = geophyte, H = hemicryptophyte, P = phanerophyte, T = therophyte. Bold corresponds to higher values of niche breadth, local abundance and regional distribution. The complete list of aliens and their invasion success’ values is in Appendix II.

Species	Origin	Life form	Local abundance	Regional distribution	Niche breadth	Invasion success
<i>Xanthium orientale</i> L.	America N	T	0.30	<b>1.00</b>	<b>0.75</b>	1.00
<i>Erigeron canadensis</i> L.	America C	T	0.24	<b>0.90</b>	<b>0.90</b>	0.99
<i>Oenothera gr. biennis</i> L.	America N	H	0.36	<b>0.85</b>	<b>0.78</b>	0.93
<i>Carpobrotus</i> N.E.Br. spp.	Africa	Ch	0.55	<b>0.81</b>	0.57	0.82
<i>Xanthium strumarium</i> L.	America S	T	0.14	<b>0.79</b>	<b>0.71</b>	0.82
<i>Amorpha fruticosa</i> L.	America N	P	0.16	0.56	<b>0.94</b>	0.78
<i>Ambrosia artemisiifolia</i> L.	America N	T	0.08	0.56	<b>0.94</b>	0.78
<i>Senecio inaequidens</i> DC	Africa	Ch / T	0.53	0.58	<b>0.74</b>	0.75
<i>Oenothera drummondii</i> Hook.	America N	H	0.44	0.52	<b>0.75</b>	0.71
<i>Oenothera glazioviana</i> Micheli	America N	H	0.45	0.45	<b>0.85</b>	0.71
<i>Oenothera parviflora</i> L.	America N	H	0.18	0.48	<b>0.87</b>	0.71
<i>Arctotheca calendula</i> L.	Africa	T	<b>0.98</b>	0.36	<b>0.81</b>	0.70
<i>Cuscuta campestris</i> Yunck	America C	T	0.21	0.48	<b>0.77</b>	0.67
<i>Prunus serotina</i> Ehrh.	America N	P	0.00	0.52	<b>0.72</b>	0.65
<i>Ambrosia psilostachya</i> DC	America N	G	0.65	0.60	0.41	0.64
<i>Rosa rugosa</i> Thunb.	Eastern Asia	P	0.08	0.51	0.66	0.62
<i>Helianthus annuus</i> L.	America N	T	0.06	0.29	<b>0.94</b>	0.60



Overall, the present work provides useful information for keeping track of the alien species which have most invasion success on coastal dunes which is a key issue in European invasion management strategies. Our list of successful alien species could be particularly valuable to plan prioritising management targets, from regional to local scales. Management planning should target first the most successful invaders and monitor emerging invasions (Nel et al. 2004). Furthermore, reported differences in local abundance, regional distribution and niche breadth should also be taken into account as they could imply different types of management strategies depending on the target aliens.

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# Appendixes

## Appendix I – Correlation matrix of the principal component analysis

**Table A1.** Correlation matrix of the principal component analysis used to calculate the synthetic index of invasion success.

	Component 1	Component 2	Component 3
Local abundance	0.23	0.96	0.14
Regional distribution	0.91	0.05	-0.40
Niche breadth	0.87	-0.31	0.38



Appendix II – Values of local abundance, regional distribution, niche breadth and invasion success

**Table A2.** Values of local abundance, regional distribution, niche breadth and invasion success, ranked from the most to the least successful species. Values are scaled between 0 and 1. Ch = chamaephyte, G = geophyte, H = hemicryptophyte, P = phanerophyte, T = therophyte.

Species	Origin	Life form	Local abundance	Regional distribution	Niche breadth	Invasion success
<i>Xanthium orientale</i> L.	America N	T	0.30	1.00	0.75	1.00
<i>Erigeron canadensis</i> L.	America C	T	0.24	0.90	0.90	0.99
<i>Oenothera</i> gr. <i>biennis</i> L.	America N	H	0.36	0.85	0.78	0.93
<i>Carpobrotus</i> N.E.Br. spp.	Africa	Ch	0.55	0.81	0.57	0.82
<i>Xanthium strumarium</i> L.	America S	T	0.14	0.79	0.71	0.82
<i>Amorpha fruticosa</i> L.	America N	P	0.16	0.56	0.94	0.78
<i>Ambrosia artemisiifolia</i> L.	America N	T	0.08	0.56	0.94	0.78
<i>Senecio inaequidens</i> DC	Africa	Ch / T	0.53	0.58	0.74	0.75
<i>Oenothera drummondii</i> Hook.	America N	H	0.44	0.52	0.75	0.71
<i>Oenothera glazioviana</i> Micheli	America N	H	0.45	0.45	0.85	0.71
<i>Oenothera parviflora</i> L.	America N	H	0.18	0.48	0.87	0.71
<i>Arctotheca calendula</i> L.	Africa	T	0.98	0.36	0.81	0.70
<i>Cuscuta campestris</i> Yunck	America C	T	0.21	0.48	0.77	0.67
<i>Prunus serotina</i> Ehrh.	America N	P	0.00	0.52	0.72	0.65
<i>Ambrosia psilostachya</i> DC	America N	G	0.65	0.60	0.41	0.64
<i>Rosa rugosa</i> Thunb.	Eastern Asia	P	0.08	0.51	0.66	0.62
<i>Helianthus annuus</i> L.	America N	T	0.06	0.29	0.94	0.60
<i>Stenotaphrum secundatum</i> (Walt.)	America C	G	0.60	0.56	0.39	0.60
<i>Cenchrus spinifex</i> Cav.	America C	T	0.21	0.53	0.54	0.60
<i>Xanthium spinosum</i> L.	America S	T	0.34	0.54	0.39	0.55
<i>Gomphocarpus fruticosus</i> (L.) R. Br.	Africa	P	0.00	0.17	1.00	0.54
<i>Matricaria discoidea</i> DC	America N	T	0.18	0.35	0.68	0.54
<i>Digitaria ciliaris</i> (Retz.) Koeler	Eastern Asia	T	0.18	0.46	0.46	0.51
<i>Symphyotrichum subulatum</i> (Spreng.) G.L. Nesom	America N	T	0.00	0.31	0.68	0.50
<i>Amaranthus retroflexus</i> L.	America N	T	0.00	0.24	0.77	0.49
<i>Xanthium pungens</i> Wallr.	America N	T	0.00	0.24	0.75	0.48
<i>Paspalum vaginatum</i> Sw.	Africa	G	0.88	0.44	0.22	0.48
<i>Oenothera oakesiana</i> (A. Gray) J.W. Robbins ex S. Watson.	America N	H	0.31	0.61	0.08	0.46
<i>Erigeron bonariensis</i> L.	America S	T	0.00	0.29	0.60	0.45
<i>Hydrocotyle bonariensis</i> Lam.	America C	G	0.68	0.35	0.32	0.44
<i>Erigeron floribundus</i> (Kunth) Sch. Bip.	America S	T	0.53	0.43	0.23	0.43
<i>Lupinus arboreus</i> Sims	America N	H	0.88	0.37	0.21	0.43
<i>Vitis rotundifolia</i> Michx.	America C	P	0.62	0.35	0.30	0.43
<i>Solanum triflorum</i> Nutt.	America N	T	0.34	0.35	0.35	0.42
<i>Spartina anglica</i> (C.E.Hubb.) P.M.Peterson & Saarela	America N	G	0.13	0.27	0.50	0.41
<i>Cenchrus longispinus</i> (Hack.) Fernald	America N	T	0.40	0.46	0.14	0.40
<i>Heterotheca subaxillaris</i> (Lam.) Britton & Rusby	America N	H	0.53	0.44	0.11	0.39
<i>Claytonia perfoliata</i> Donn ex Willd.	America N	T	0.27	0.44	0.18	0.39
<i>Yucca gloriosa</i> L.	America N	P	0.67	0.27	0.25	0.36
<i>Amaranthus albus</i> L.	America N	T	0.00	0.10	0.67	0.36
<i>Oenothera fallax</i> Soldano & Rostański	America N	H	0.52	0.45	0.01	0.35
<i>Agave americana</i> L.	America C	P	0.25	0.21	0.43	0.35
<i>Erigeron sumatrensis</i> Retz.	America S	T	0.00	0.21	0.50	0.35
<i>Robinia pseudoacacia</i> L.	America N	P	0.00	0.10	0.62	0.34
<i>Lycium barbarum</i> L.	Eastern Asia	P	0.50	0.10	0.45	0.32
<i>Oxalis pescaprae</i> L.	Africa	G	0.38	0.33	0.11	0.30
<i>Oenothera suaveolens</i> Desf. ex Pers.	America N	H	0.40	0.40	0.00	0.30
<i>Sporobolus indicus</i> (L.) R. Br.	America C	H	0.60	0.24	0.17	0.30
<i>Epilobium ciliatum</i> Raf.	America N	H	0.00	0.17	0.41	0.28
<i>Oenothera ammophila</i> Focke	America N	H	0.36	0.36	0.00	0.27
<i>Ambrosia tenuifolia</i> Spreng.	America S	G	0.67	0.27	0.00	0.25



<i>Cortaderia selloana</i> (Schult. & Schult. f.) Asch. & Graebn.	America S	H	0.00	0.17	0.33	0.25
<i>Epilobium brunnescens</i> (Cockayne) P. H. Raven & Engelhorn	Oceania	H	0.75	0.21	0.01	0.23
<i>Populus balsamifera</i> L.	America N	P	0.00	0.29	0.00	0.19
<i>Oenothera longiflora</i> L.	America S	H	0.20	0.24	0.00	0.18
<i>Elaeagnus commutata</i> Bernh. ex Rydb.	America N	P	0.00	0.24	0.00	0.15
<i>Solanum linnaeanum</i> Hepper & P.-M.L. Jaeger	Africa	P	0.00	0.17	0.10	0.15
<i>Cycloloma atriplicifolium</i> (Spreng.) J.M. Coult.	America N	T	0.00	0.21	0.00	0.13
<i>Lepidium densiflorum</i> Schrad.	America N	H	1.00	0.00	0.00	0.12
<i>Amsinckia menziesii</i> (Lehm.) A. Nelson & J.F. Macbr.	America N	P	1.00	0.00	0.00	0.12
<i>Populus trichocarpa</i> Torr. & A.Gray ex. Hook.	America N	P	1.00	0.00	0.00	0.12
<i>Pseudognaphalium undulatum</i> L.	Africa	T	1.00	0.00	0.00	0.12
<i>Solanum tuberosum</i> L.	America S	T	1.00	0.00	0.00	0.12
<i>Juncus tenuis</i> Willd.	America N	H	0.00	0.17	0.00	0.10
<i>Tetragonia tetragonoides</i> (Pall.) Kuntze	Eastern Asia	T	0.20	0.10	0.00	0.09
<i>Suaeda foliosa</i> Moq.	America S	Ch	0.00	0.10	0.04	0.09
<i>Vaccinium macrocarpon</i> Ait.	America N	P	0.00	0.10	0.01	0.07
<i>Hypericum canadense</i> L.	America N	P	0.00	0.10	0.00	0.07
<i>Heliotropium curassavicum</i> L.	America C	Ch	0.00	0.10	0.00	0.07
<i>Symphyotrichum novibelgii</i> (L.) G.L. Nesom	America N	H	0.00	0.10	0.00	0.07
<i>Aloe maculata</i> All.	Africa	P	0.00	0.10	0.00	0.07
<i>Symphoricarpos albus</i> (L.) S.F. Blake	America N	P	0.00	0.10	0.00	0.07
<i>Setaria italica</i> (L.) P. Beauv.	Eastern Asia	T	0.00	0.10	0.00	0.07
<i>Solidago canadensis</i> L.	America N	H	0.40	0.00	0.00	0.05
<i>Oenothera rubricaulis</i> Kleb.	America N	H	0.00	0.00	0.00	0.00
<i>Oenothera stricta</i> Ledeb. ex Link	America S	H	0.00	0.00	0.00	0.00
<i>Symphyotrichum lanceolatum</i> (Willd.) G.L. Nesom	America N	H	0.00	0.00	0.00	0.00
<i>Eschscholzia californica</i> L.	America N	H / T	0.00	0.00	0.00	0.00
<i>Phytolacca acinosa</i> Roxb.	Eastern Asia	Ch / H	0.00	0.00	0.00	0.00
<i>Ailanthus altissima</i> (Mill.) Swingle	Eastern Asia	P	0.00	0.00	0.00	0.00
<i>Baccharis halimifolia</i> L.	America C	P	0.00	0.00	0.00	0.00
<i>Lonicera japonica</i> Thunb.	Eastern Asia	P	0.00	0.00	0.00	0.00
<i>Mahonia aquifolium</i> (Pursh) Nutt.	America N	P	0.00	0.00	0.00	0.00
<i>Opuntia ficusindica</i> (L.) Mill.	America C	P	0.00	0.00	0.00	0.00
<i>Amaranthus blitoides</i> S. Watson	America N	T	0.00	0.00	0.00	0.00
<i>Datura stramonium</i> L.	America C	T	0.00	0.00	0.00	0.00
<i>Iva xanthifolia</i> Nutt.	America N	T	0.00	0.00	0.00	0.00
<i>Lepidium didymum</i> L.	America S	T	0.00	0.00	0.00	0.00